Pacific Science (1990), vol. 44, no. 1: 38–50

Primary Production in the Columbia River Estuary II. Grazing Losses, Transport, and a Phytoplankton Carbon Budget[1]

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ABSTRACT: Mean loss of phytoplankton carbon as a result of microcrustacean grazing ranged from 0.03 to 8.94 mg C m^{-3} day^{-1}, depending upon time of year and location in the estuary. On an annual basis, median grazing rate was 1893 mt C yr^{-1}, which represented 6.3% of the annual primary production in the estuary. Daily transport of phytoplankton carbon decreased from the fluvial regions to the ocean, with the largest decrease occurring at the freshwater–brackish water interface. Annual import to the study area from upriver (excluding the May 1980 data, which were affected by the eruption of Mt. Saint Helens) was 61,440 mt C yr^{-1}, while annual export to the ocean was 40,560 mt C yr^{-1}. Total phytoplankton carbon input to the estuary was 91,316 mt C yr^{-1}, a summation of import from upriver and in situ primary production (29,876 mt C yr^{-1}, from a previous report). Export to the ocean plus median in situ grazing loss equalled 42,453 mt C yr^{-1}, so that there was an unaccounted balance of 48,863 mt C yr^{-1}. Some of this was night-time respiratory loss from the phytoplankton, estimated at 12,209 mt C yr^{-1}. If the standing stock of phytoplankton carbon in the estuary was reasonably in steady state on an annual basis, the remaining balance must have been satisfied by conversion of phytoplankton carbon to non-chlorophyllous detrital particulate carbon (mostly at the freshwater–brackish water interface) and/or by conversion to dissolved organic carbon during transit through the estuary. Some indirect evidence suggests that phytoplankton carbon was mainly converted to detrital particulate carbon during the short transit time through the estuary, but verification requires further data.

Lara-Lara et al. (1990) presented evidence that the Columbia River estuary is a system in which in situ phytoplankton production is kept low by (1) the short residence time of cells in the estuary; (2) light limitation as a result of a shallow euphotic zone; and (3) loss of viable freshwater cells on encountering slightly saline water during transit through the estuary in summer. However, Simenstad and Cordell (1985) and Jones et al. (in press) have shown, respectively, that large concentrations of epibenthic and water-column zooplankton often occur in the estuary, which suggests that a substantial fraction of the phytoplankton produced in the estuary might be removed by grazing. Peaks of epibenthic zooplankton exceed 150×10^3 individuals per m^2 on occasion, and even during winter concentrations of 5×10^3 m^{-2} are not uncommon. Suspension-feeding zooplankton (mainly *Eurytemora affinis*) can number over 100×10^3 individuals per m^2 in the mixing zone in spring and summer. On the other hand, Lara-Lara et al. (1990) suggested that large amounts of particulate organic matter transported into the es-

[1] This study was supported by a grant from the Pacific Northwest River Basins Commission and the U.S. Water Resources Council, administered through the Columbia River Estuary Data Development Program (CREDDP) and the Columbia River Estuary Study Taskforce (CREST). J. R. Lara-Lara had a scholarship from the National Council of Science and Technology in México. Manuscript accepted 12 May 1989.

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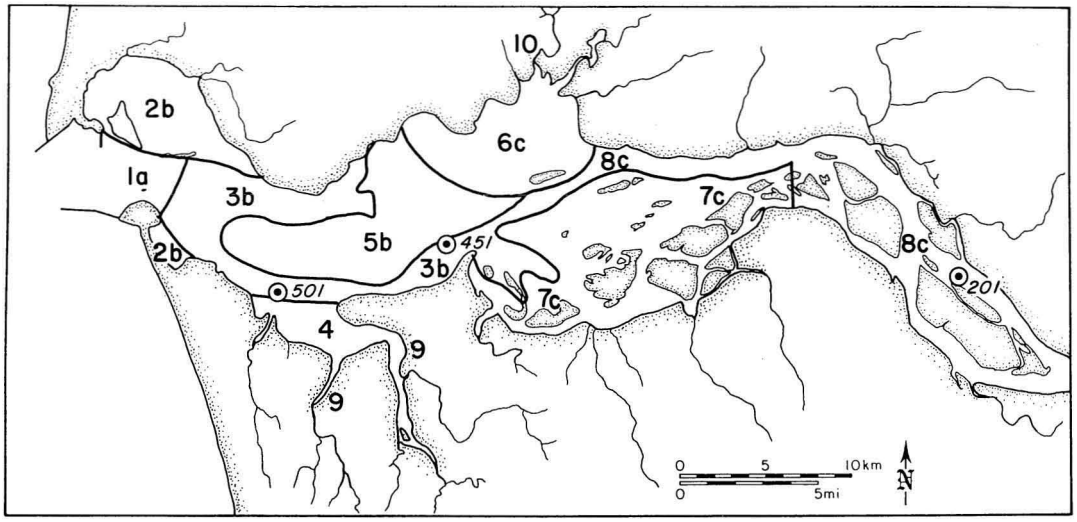

FIGURE 1. Map of the study area. Estuarine regions (numbers) and zones (letters) based on hydrographic and sedimentary properties. Zones are (a) marine zone, (b) estuarine mixing zone, and (c) freshwater, or tidal fluvial, zone. Locations of zooplankton collections for the grazing experiments are shown (stations 501, 451, and 201).

tuary from upriver likely supplement the in situ particle production and add to the food rations available to filter-feeders. In this paper we evaluate grazing losses and transport of phytoplankton in the Columbia River estuary and present a phytoplankton budget in terms of carbon.

MATERIALS AND METHODS

The division of the study area into three zones and 10 regions was the same as that presented in Lara-Lara et al. (1990) (Figure 1). Stations sampled through all seasons for chlorophyll *a* and other particle properties were also the same as reported in Lara-Lara et al. (1990), but grazing experiments were performed with zooplankton collected only during June and July 1981 from stations 501, 451, and 201 (Figure 1).

Methods for measuring zooplankton grazing on natural particles were adapted from Haney (1971), Daro (1978), Griffiths and Caperon (1979), and Roman and Rublee (1981). For each experiment, 8 liters of water at a given sampling station were filtered through 64-μm-mesh Nitex netting into a transparent polyethylene container, and 60 μCi l^{-1} of $NaH^{14}CO_3$ were added. The container was then incubated for 1 day under natural light in a temperature-controlled water bath. Zooplankton were collected during this incubation period by making many short net hauls (250-μm mesh). The contents of each net haul were placed into a battery jar so that swimming zooplankton could be gently decanted into a holding flask containing filtered estuarine water with chlorophyll levels brought up to natural levels in the estuary. To begin each experiment, 25–30 zooplankton were placed into bottles containing 200 ml of the labeled phytoplankton suspension. All bottles were covered with aluminum foil and placed into the temperature-controlled water bath, except during one experiment in June in which the bottles were not covered with foil. Bottles were then harvested at 0, 0.25, 0.50, 0.75, 1, 1.50, 2, 3, 4, 6, 17, 19, 21, and 24 hr to develop a time series of carbon-14 accumulation in the zooplankton grazing on labeled cells. After each experimental time period, zooplankton were gently seived onto 153-μm-mesh Nitex netting, and the phytoplankton were collected on 0.45-μm-pore-size Millipore filters. The zooplankton were gently washed with filtered

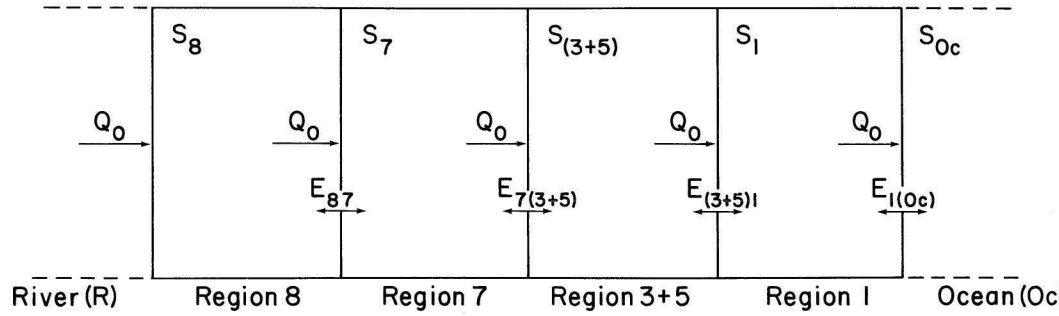

FIGURE 2. Two-parameter model of the Columbia River estuarine continuum, used to evaluate horizontal exchanges (E) between adjacent regions (based on salt transport). S = salinity (‰); Q = river flow (m^3 sec^{-1}).

estuarine water, and six individuals of each of the two dominant groups (copepods and cladocerans) were selected under a binocular microscope and placed in individual scintillation vials containing tissue solubilizer, for later determination of their carbon-14 activities. The filters with the phytoplankton were placed directly into vials containing Aquasol. No significant differences were found when we compared fumed (HCl) and unfumed carbon-14 samples. This was expected, because the estuarine phytoplankton were mainly diatoms and microflagellates (Amspoker and McIntire 1986). Both phytoplankton and zooplankton were analyzed for carbon-14 in a liquid scintillation counter. Controls were run in which zooplankton were subjected to carbon-14 over a time course without phytoplankton present to test adsorption, and in which the time course of phytoplankton carbon-14 activity was monitored in the absence of zooplankton.

Transport of phytoplankton biomass from upriver to the sea was estimated by calculating chlorophyll transports through region 8 (see Figure 1), and then, in sequence, through regions 7, (3 + 5), and 1. As in the study by Lara-Lara et al. (1990), regions 3 and 5 were considered as one because mean chlorophyll concentrations in both regions were indistinguishable. Transport through region 1 to the ocean was considered less accurate than the other transport calculations because chlorophyll concentrations in the adjacent ocean were taken from historical data. A two-parameter box model based on salt transport, which assumed complete vertical mixing along the length of the river-estuary continuum, was used to evaluate horizontal exchange between each adjacent region (Officer 1980). Although complete vertical mixing of salinity (and small chlorophyllous particles) was not achieved throughout the estuary, particularly in region 1 (Jay and Smith, in press; Lara-Lara et al. 1990), use of more complex models (Officer 1980) did not change final chlorophyll transport calculation by more than a few percentage points at any time. The parameters required to estimate the exchange rates are shown in Figure 2. The equations for estimating the exchange rates between the river (R) and region 8 (E_{R8}), between regions 8 and 7 (E_{87}), between 7 and (3 + 5) [$E_{7(3+5)}$], between (3 + 5) and 1 [$E_{(3+5)1}$], and between 1 and the ocean [$E_{1(OC)}$] are as follows:

$$E_{R8} = Q_0 S_R/(S_8 - S_R) \quad (1)$$

$$E_{87} = Q_0 S_8/(S_7 - S_8) \quad (2)$$

$$E_{7(3+5)} = Q_0 S_7/[S_{(3+5)} - S_7] \quad (3)$$

$$E_{(3+5)1} = Q_0 S_{(3+5)}/[S_1 - S_{(3+5)}] \quad (4)$$

$$E_{1(OC)} = Q_0 S_1/(S_{(OC)} - S_1) \quad (5)$$

where Q is river flow (m^3 sec^{-1}), S is salinity (‰), and E is the exchange between regions (m^3 sec^{-1}), with subscripts referring to the specific regions. Evaluations of all parameters are given in Table 1 for high-flow sampling months (April and May), low-flow months (July and September), and winter months (November and February). Best esti-

TABLE 1

VALUES FOR PARAMETERS USED TO ESTIMATE EXCHANGE RATES (E) BETWEEN REGIONS, AND COMPUTED VALUES OF E (m^3 sec^{-1}) BETWEEN UPRIVER, REGIONS 8, 7, (3 + 5), AND 1, AND THE OCEAN

PARAMETER	(UNITS)	APR. 1980	MAY 1980	JULY 1980	SEPT. 1980	NOV. 1980	FEB. 1981
Q_0	(m^3 sec^{-1} × 10^3)	9.2	10.7	6.0	2.7	4.0	7.4
S_8	(‰)	0	0	0	0	0	0
S_7	(‰)	0	0	0	0	0	0
$S_{(3+5)}$	(‰)	5.67	5.67	9.66	9.66	6.50	6.50
S_1	(‰)	15.24	15.24	23.80	23.80	16.50	16.50
S_{OC}	(‰)	32.70	32.70	32.70	32.70	32.20	32.20
E_{R8}	(m^3 sec^{-1} × 10^3)	0	0	0	0	0	0
E_{87}	(m^3 sec^{-1} × 10^3)	0	0	0	0	0	0
$E_{7(3+5)}$	(m^3 sec^{-1} × 10^3)	0	0	0	0	0	0
$E_{(3+5)1}$	(m^3 sec^{-1} × 10^3)	5.45	6.34	4.10	1.84	2.60	4.81
$E_{1(OC)}$	(m^3 sec^{-1} × 10^3)	8.03	9.34	16.04	7.22	4.20	7.78

mates of river flows and salinities were obtained from Jay and Smith (in press) and the U.S. Geological Survey (1980, 1981).

Because salinity was zero in the freshwater regions, exchanges of chlorophyllous particles between the river and region 8, between regions 8 and 7, and between regions 7 and (3 + 5) were considered to be zero (Table 1). Transport thus was governed solely by river flow (Q_0) and chlorophyll concentration (C). For example, transport of chlorophyll into region 7 from region 8 was

$$T_{87} = Q_0 C_8 \tag{6}$$

where T is chorophyll transport (mg sec^{-1}) and C is chlorophyll concentration (mg m^{-3}) in region 8. On the other hand, when salinity was non-zero the exchange terms were also non-zero, as per example in the chlorophyll transport from region (3 + 5) to region 1:

$$T_{(3+5)1} = Q_0 C_{(3+5)} + E_{(3+5)1}[C_{(3+5)} - C_1] \tag{7}$$

where $E_{(3+5)1}$ is calculated from equation 4 and given in Table 1 for the different months.

Chlorophyll-based rates were converted to carbon-based rates via a C : Chl ratio of 40 developed for the Columbia River estuary (Lara-Lara 1982). Basing all data on carbon allowed us to develop a phytoplankton carbon budget for the estuary.

RESULTS

Grazing Removal

The accumulation of carbon-14 by mixed copepods (mainly *Eurytemora affinis*) and two genera of cladocerans (*Bosmina longirostris* and *Daphnia* spp.) is shown in Figure 3 for all experiments. The per-animal uptake curves appeared similar. Filtering rates were calculated using only the uptake values for the first hour, however, to reduce the probability of including carbon-14 loss via fecal pellet production in the filtering rate calculation. Fifty percent of the chlorophyll in copepod intestinal tracts has been reported to be evacuated (presumably as fecal pellets) in about $\frac{1}{2}$ to 3 hr (Dagg and Grill 1980, Hayward 1980, Kiorboe et al. 1982, Dagg and Wyman 1983, Batchelder 1985, Wang and Conover 1986). We considered that carbon-14 uptake by our Columbia estuary zooplankton after 1 hr could have been affected by egestion of carbon-14, and so we did not use uptake data beyond that time.

Daily filtering rates were calculated for both copepods and cladocerans according to the formula:

$$f = \left(\frac{a}{ph}\right)\left(\frac{24\ hr}{day}\right) \tag{8}$$

where f = filtering rate (ml $animal^{-1}$ day^{-1}); a = 14-C disintegrations min^{-1} (dpm) per ani-

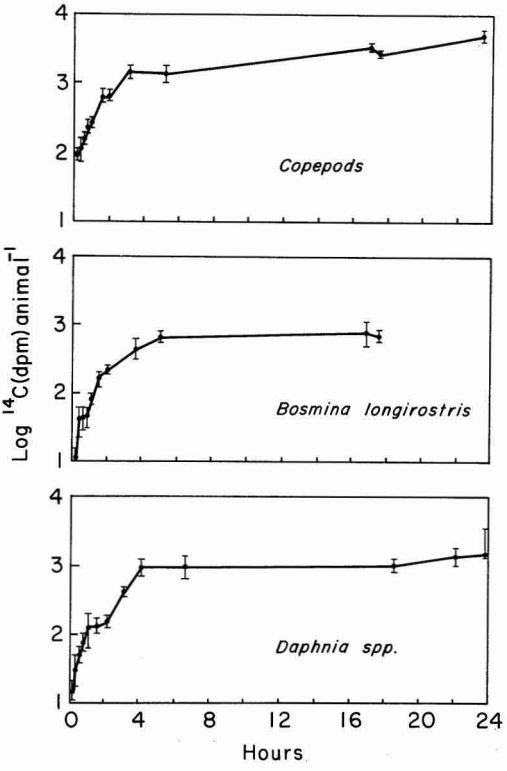

FIGURE 3. Time series of mean zooplankton accumulation of carbon-14 from prelabeled phytoplankton by the three most common taxa in the Columbia River estuary. Bars indicate ± 1 SE of the mean.

mal over the first hour of uptake, corrected for the very small amount of 14-C accumulation by animals in 14-C medium without algal cells; p = dpm per ml of phytoplankton suspension, which did not measureably change over the first hour; and h = hours of feeding in the experiment (1 hr). The formula above assumes that f is continuous throughout the 24-hr day, which may yield some overestimate of the "true" daily filtering rate. There were no significant differences between the filtering rates for any given grazer group at the three stations within any given month and no differences between the two months for the copepods (Table 2); however, significant differences were observed between *Bosmina longirostris* and the other two groups. The filtering rates of the copepods and *Daphnia* spp. together averaged 1.24 ± 0.26 ml animal^{-1} day^{-1}, while those for *B. longirostris* averaged half of that (0.60 ± 0.21 ml animal^{-1} day^{-1}). There was a slight trend toward higher filtering rates in the nondarkened grazing vessels than in the darkened ones, but the data are too few to analyze further.

Total phytoplankton removed from the estuary by grazing can be estimated if one knows zooplankton and phytoplankton concentrations in the estuary as well as the zooplankton filtration rates. No detailed distribu-

TABLE 2

MEAN FILTRATION RATES FOR THE THREE MOST ABUNDANT TAXA IN THE COLUMBIA RIVER ESTUARY $\pm$ 1 SE (n = SIX ANIMALS PER STATION)

			f (ml ANIMAL^{-1} DAY^{-1})	
GROUP	STATION	CONDITION	JUNE	JULY
Copepods	501	Dark	1.03 ± 0.25	1.62 ± 0.25
	451	Dark	1.00 ± 0.13	0.93 ± 0.40
	201	Dark	1.10 ± 0.24	1.53 ± 0.31
	201	Light	1.50 ± 0.20	
			Mean 1.16 ± 0.19	1.36 ± 0.32
B. longirostris	501	Dark	0.61 ± 0.24	
	451	Dark	0.32 ± 0.03	
	201	Dark	0.55 ± 0.19	
	201	Light	0.90 ± 0.40	
			Mean 0.60 ± 0.21	
Daphnia spp.	451	Dark		1.26 ± 0.32
	201	Dark		1.19 ± 0.22
				Mean 1.22 ± 0.27

tional studies for zooplankton exist in the Columbia River estuary. For our purposes we arrayed the available literature data (Haertel 1970, Misitano 1974, Jones et al. [in press]) and calculated median concentrations and concentration ranges by season and general habitat. Most of the data in the arrays came from Jones et al. (in press) and were taken during the same years (1980, 1981) of our study. The large populations in the estuarine regions in spring and summer, and in the marine region in spring, were composed chiefly of *Eurytemora affinis*. For most of the spring and summer we used a zooplankton filtration rate of 1.2 ml animal^{-1} day^{-1} (Table 3a). Because *Bosmina longirostris* was a minor fraction of the yearly estuarine zooplankton composition, except in the freshwater regions in spring, the rate used was close to the composite rate for copepods and *Daphnia* spp. In the freshwater regions in spring we used a filtration rate of 0.9 ml animal^{-1} day^{-1}, midway between the rates for *Bosmina* and the other taxa. We have no direct data on winter filtration rates in the Columbia estuary, but other studies have shown that grazing rates, levels of digestive enzymes, and other metabolic rates all tend to decrease as the animals move into the overwintering condition (Conover 1962, Martin 1970, Marshall 1973, Poulet 1974, Hallberg and Hirche 1980, Hirche 1983, Downs and Lorenzen 1985). We have chosen a winter filtration rate of 0.6 ml animal^{-1} day^{-1}. Ultimately, this choice is of little consequence to total grazing removal of phytoplankton in the estuary (see below), because both zooplankton and phytoplankton concentrations in winter are low, relative to concentrations at other times of the year.

Mean concentrations of phytoplankton carbon were computed by season and estuarine zone (Table 3b), using the data from Lara-Lara et al. (1990). The general decrease in phytoplankton biomass from fresh water to

TABLE 3

a., MEDIAN CONCENTRATIONS OF ZOOPLANKTON (NO. m^{-3}); b., MEAN PHYTOPLANKTON CARBON CONCENTRATIONS (mg C m^{-3}) ± SE OF THE MEAN

ZONE	SEASON					
	SPRING		SUMMER		FALL, WINTER	
a.						
Fresh water	2.5×10^3		5.9×10^3		0.8×10^3	
(regions 7, 8)	[10^3–10^4]	0.9	[10^3–(5×10^4)]	1.2	[10^2–10^3]	0.6
Mixing	23.0×10^3		10.3×10^3		1.0×10^3	
(regions 3, 5)	[10^2–(5×10^4)]	1.2	[10^2–(5×10^4)]	1.2	[10^2–10^3]	0.6
Marine	13.8×10^3		3.1×10^3		0.6×10^3	
(region 1)	[10^3–(5×10^4)]	1.2	[10^3–10^4]	1.2	[10^2–10^3]	0.6
b.						
Fresh water (regions 7, 8)	474 ± 177		552 ± 17		209 ± 51	
Mixing (regions 3, 5)	324 ± 108		236 ± 62		129 ± 43	
Marine (region 1)	200 ± 21		272 ± 38		72 ± 25	

NOTE: Numbers in brackets are the approximate ranges of individual collections. The value in the small square in the bottom right corner of each box is the filtration rate (ml animal^{-1} day^{-1}) assigned with each animal concentration.

*May 1980 data not included.

TABLE 4

MEDIAN DAILY PHYTOPLANKTON CARBON REMOVAL, AND ANNUAL REMOVAL, BY ZOOPLANKTON GRAZING IN THE COLUMBIA RIVER ESTUARY (RANGES ARE GIVEN IN PARENTHESES)

SEASON	ZONE	FILTRATION RATE* (% DAY^{-1})	GRAZING REMOVAL† (mg C m^{-3} DAY^{-1})	ANNUAL GRAZING REMOVAL‡ (mt C SEASON^{-1})
Spring	Freshwater	0.23 (0.09–0.90)	1.09 (0.43–4.27)	70.77 (27.92–277.24)
	Mixing	2.76 (0.01–6.00)	8.94 (0.03–19.44)	1,158.63 (3.89–1,262.21)
	Marine	1.66 (0.12–6.00)	3.32 (0.24–12.00)	132.45 (9.57–478.73)
				Σ = 1,361.85
Summer	Freshwater	0.71 (0.12–6.00)	3.92 (0.66–33.12)	191.93 (32.32–1,621.63)
	Mixing	1.24 (0.01–6.00)	2.93 (0.02–14.16)	286.35 (1.95–1,383.88)
	Marine	0.37 (0.12–1.20)	1.01 (0.33–3.26)	30.38 (9.93–98.07)
				Σ = 508.66
Fall, Winter	Freshwater	0.05 (0.01–0.12)	0.10 (0.02–0.25)	8.04 (1.61–20.09)
	Mixing	0.06 (0.01–0.12)	0.08 (0.01–0.15)	12.83 (1.60–24.06)
	Marine	0.04 (0.01–0.12)	0.03 (0.01–0.09)	1.48 (0.49–4.44)
				Σ = 22.35
				Σ = 1,892.86 mt C yr^{-1}

*Product of zooplankton concentration (no. m^{-3}, from Table 3) and mean filtration rate (ml animal^{-1} day^{-1}, from Table 3), expressed as a percentage.
†Product of filtration rate (% day^{-1}) and phytoplankton carbon concentration (mg C m^{-3}, from Table 3).
‡(mg C m^{-3} day^{-1}) × (m^3 in the particular region) × (no. days in the particular season) ÷ 10^9 mg mt^{-1}.

the marine zone is evident, as well as the pronounced decease between the freshwater and mixing zones in summer as a result of phytoplankton cell lysis as the cells contact low-salinity water during downstream transport (Lara-Lara et al. 1990).

The data in Table 3 allow rough computation of median daily phytoplanton carbon removal by zooplankton in the Columbia River estuary and ultimately lead to an estimate of annual removal by grazing (Table 4). The large ranges in rates, particularly in spring and summer, mainly reflect the large ranges in zooplankton concentration estimates. As expected, grazing removal was highest in spring and summer, up to 6% of the phytoplankton crop per day by concentrated patches of zooplankton. The greatest removal was in the estuarine and marine regions in spring, principally as a result of large concentrations of *Eurytemora affinis* in these areas (Jones et al. [in press]). In summer, the *E. affinis* population tended to shift to estuarine and riverine areas, and grazing removal was heaviest there at that time. Winter grazing removal was very low, as anticipated. Even if the winter filtration rate of 0.6 ml animal^{-1} day^{-1} were doubled the median grazing removal (mg C m^{-3} day^{-1}) would still be relatively inconsequential (about 5% of the comparable median summer rates).

Phytoplankton Transport

Transport rates of phytoplankton carbon (mg sec^{-1}) for each region and sampling date were scaled up to mt C day^{-1} (Table 5). The rates decreased from region 8 through region (3 + 5) on all sampling dates. Further decrease in these rates through region 1 to the adjacent ocean was noted in all months except July 1980; however, the use of historical phytoplankton concentrations in the adjacent ocean to compute the rates through region 1 made these rates more uncertain. The large decrease in transport between regions 7 and (3 + 5) in May and July again was the result of losing freshwater phytoplankton at the freshwater–brackish water interface.

It should be noted that the May 1980 transports likely were inflated to some degree by the added material from the Mt. Saint Helens eruption. Integrating the daily transports through region (3 + 5) over a full

TABLE 5

DAILY TRANSPORT OF PHYTOPLANKTON-DERIVED ORGANIC CARBON (PPOC) THROUGH SUCCESSIVE REGIONS DOWN THE MAIN AXIS OF THE COLUMBIA RIVER ESTUARY, FOR EACH SAMPLING MONTH

	TRANSPORT RATES (mt C DAY^{-1})				
MONTH	T_{R8} RIVER	T_{87} REGION 8	$T_{7(3+5)}$ REGION 7	$T_{(3+5)1}$ REGION (3 + 5)	$T_{1(OC)}$ REGION 1*
Apr. 1980	255.6	251.2	238.5	224.8	(214.5)
May	666.1	654.5	628.6	434.4	—
July	304.1	290.3	288.2	117.3	(179.1)
Sept.	69.7	68.1	48.5	47.2	(43.0)
Nov.	75.3	71.9	48.4	32.1	(15.3)
Feb. 1981	134.2	133.0	125.3	106.8	(60.2)

Estimated annual import from the river into region 8 (without May): 61,440 mt C yr^{-1}.
Estimated annual import from the river into region 8 (including May): 76,395 t C yr^{-1}.
Estimated annual export through region (3 + 5) to region 1 (without May): 41,430 mt C yr^{-1}.
Estimated annual export through region (3 + 5) to region 1 (including May): 45,960 mt C yr^{-1}.
Estimated annual export through region 1 to ocean (without May): 40,560 mt C yr^{-1}.
*Estimates in parentheses (region 1) are based on literature values for chlorophyll concentrations in the near ocean off the Columbia River, taken in different years. No export through region 1 in May could be estimated because of the lack of data in adjacent ocean water after the volcanic explosion.

year with and without the May rates yielded rough annual transports that differed by 4350 mt C yr^{-1}, an approximate 11% change. Estimated annual export to the ocean (without May data) was 40,560 mt C yr^{-1}, only 870 mt yr^{-1} less than the transport into region 1 from region (3 + 5); thus, apparently very little phytoplanktonic carbon is lost during transport through region 1. Most of the phytoplankton cells in region 1 are marine or euryhaline species (Amspoker and McIntire 1986).

Annual Phytoplankton Carbon Budget

Combining the in situ production data of Lara-Lara et al. (1990) with the grazing and transport data herein allows formulation of an annual phytoplankton carbon budget. The two input terms are in situ primary production and transport of phytoplankton carbon into the estuary. Excluding May 1980 data, annual primary production in the study area was 29,876 mt C (Lara-Lara et al. 1990). This was net or near-net production during the daylight period throughout the year, without accounting for night-time respiratory loss of carbon. Import of phytoplankton carbon from the main stem of the river into region 8 (T_{R8}) was 61,440 mt C yr^{-1} (Table 5). Although areal primary production in a few small tributaries to the estuary was high in spring and summer, the volume contribution of these small tributaries was low, and their effect in the main estuary was unmeasureable (Lara-Lara et al. 1990). As a further check on the unimportance of tributary flow into the estuary, we compared monthly mean flows at the estuary mouth with those 120 km upstream (U.S. Geological Survey 1980, 1981), well beyond our study area (Figure 4). The

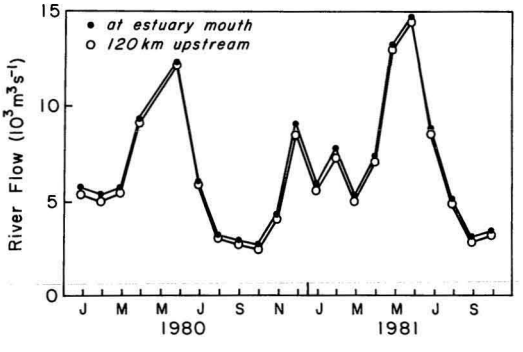

FIGURE 4. Monthly means of Columbia River flow at the mouth of the estuary and 120 km upstream, for the period of sampling.

almost perfect overlay of the flow rates attested to the extreme dominance of the main river axis over the small tributaries.

Summation of in situ production (29,876 mt C yr^{-1}) and transport into region 8 (61,440 mt C yr^{-1}) yielded a total phytoplankton carbon input of 91,316 mt yr^{-1}. Export to the ocean [$T_{1(OC)}$] was 40,560 mt C yr^{-1} (Table 5), and median grazing loss in the estuary was 1893 mt C yr^{-1} (Table 4). Under steady state, there was an unaccounted balance of

$$(61{,}440 + 29{,}876) - (40{,}560 + 1893) = 48{,}863 \text{ mt C yr}^{-1} \quad (9)$$

Some of this was night-time respiratory loss of carbon by the phytoplankton. We have no direct estimates of this loss, but Davis and McIntire (1983) found that respiration of sediment-associated algae in the Yaquina River estuary, Oregon, averaged 29% of gross production. Laboratory data on both marine (Laws and Bannister 1980) and freshwater (Bidwell 1976) species suggested that respiration rates varied between about 10 and 30% of daylight carbon production. If we assume that respiration was 29% of daylight gross production in the Columbia estuary, and that the rate was applicable during the night as well as during daylight hours throughout the year, then we can estimate the 24-hr production for each sampling month by subtracting night-time respiratory loss from net daylight production. Integration of monthly 24-hr rates through the year yielded an estimate of 17,667 mt C yr^{-1}, which was an estimate of the annual 24-hr production in the Columbia estuary. Thus, night-time respiration was estimated to account for $29{,}876 - 17{,}667 = 12{,}209$ mt C yr^{-1} on average, which was almost 41% of the 29,876 mt C annual net daylight production. The unaccounted balance (equation 9) can be reduced to $48{,}863 - 12{,}209 = 36{,}654$ mt C yr^{-1} after night-time respiration is accounted for by the above model. If we assume that respiration averaged 10% of gross production (rather than 29%), an average annual night-time respiration of 3322 mt C yr^{-1} would be computed. This estimate would be only 11% of the 29,876 mt C annual net daylight production. The unaccounted balance (equation 9) under this scenario of reduced respiration would be $48{,}863 - 3322 = 45{,}541$ mt C yr^{-1}. The uncertainty in the annual night-time respiration term thus leads to uncertainty in the unaccounted carbon balance in the estuary, with the unaccounted balance most likely falling somewhere in the range of 36,654 to 45,541 mt C yr^{-1}.

The median annual grazing removal term (1893 mt C yr^{-1}) was also widely variable; however, even if one computes the highest conceivable estimate (by summing all annual top-of-the-range estimates in Table 4), the value (5172 mt C yr^{-1}) was still relatively small and could not account for much of the unaccounted balance of 36,654 (or 45,541) mt C yr^{-1}. This balance must be satisifed by conversion of phytoplankton carbon to non-chlorophyllous detrital particulate carbon (mostly at the freshwater-brackish water interface), and/or by conversion to dissolved organic carbon during transit through the estuary. Some of the detrital particulate carbon must settle to the bottom where it provides food ration for benthic organisms, and some must be transported out of the estuary.

DISCUSSION

Estimates of zooplankton filtration rates vary depending upon grazer size and physiological state; upon concentration, size, and quality of food particles; upon environmental variables; and upon experimental techniques. Despite all these effects, filtering rates of zooplankton in the Columbia River estuary were in line with values previously reported for other freshwater or estuarine macrozooplankton (Table 6). Grazing removal by Columbia estuary zooplankton ranged between 0.01 and 6% day^{-1} of the phytoplankton standing stock and, on average, represented $(1893/29{,}876) \times 100 = 6.3\%$ of annual primary production in the estuary. However, we did not measure the grazing pressure due to the microzooplankton, which in recent studies has been shown to be important in coastal and estuarine ecosystems (Capriulo and Carpenter 1980, Landry and Hassett 1982, Suttle et al. 1986, Verity 1986, Burkill et al. 1987). Graz-

TABLE 6

REPORTED FILTERING RATES FOR REPRESENTATIVE ZOOPLANKTON TAXA FOUND IN THE COLUMBIA RIVER ESTUARY

ZOOPLANKTON	FOOD	ml ANIMAL^{-1} DAY^{-1}	REFERENCES
Acartia clausi	>10 μM diatoms	2.7	Marshall and Orr (1962)
Acartia longiremis	Natural phytoplankton	0.4–6.1	Taguchi and Fukuchi (1975)
Pseudocalanus minutus	Natural phytoplankton	0.4–6.1	Taguchi and Fukuchi (1975)
Oithona similis	>10 μM flagellates	0.02	Marshall and Orr (1962)
Diaptomus graciloides	Natural phytoplankton	1.0–3.0	Nauwerck (1959)
Diaptomus oregonensis	Natural phytoplankton	1.5–12.9	McQueen (1970)
Mixed copepods*	Natural phytoplankton	0.9–1.6	This study
Daphnia spp.†	Natural phytoplankton	1.2	This study
Daphnia rosea	Natural phytoplankton	0.9–6.7	Burns and Rigler (1967)
Daphnia galeata mendotae	Natural phytoplankton	1.1–6.2	Burns and Rigler (1967)
Daphnia longispina	Natural phytoplankton	0.5–4.6	Nauwerck (1963)
Daphnia pulex	*Chlamydomonas*	0.9–5.1	Richman (1958)
Bosmina longirostris	Yeast, bacteria, algae	0.2–0.9	Haney (1973)
Bozmina longirostris	Natural phytoplankton	0.3–0.6	This study

*Dominant species were *Eurytemora affinis*, *Diaptomus* spp., and *Canuella canadensis*.
†Dominant species were *Daphnia longispina* and *D. pulex*.

ing removals of relatively low magnitudes by macrozooplankton apparently are characteristic of shallow estuarine and coastal waters. For example, Heinle (1974) found that the large populations of *Acartia tonsa* in the Patuxent River estuary grazed only between 2.5 to 7.4% day^{-1} of the total algal biomass. Williams et al. (1968) estimated that zooplankton in the estuarine system at Beaufort, North Carolina grazed 2 to 9% of the phytoplankton net production, while Nicolajsen et al. (1983) showed that 1 to 5% of the net primary production was channeled through zooplankton in the Oresund, Denmark. Riley (1959) estimated that grazing removal accounted for only 4 to 6% day^{-1} of the phytoplankton population available in Block Island Sound and Long Island Sound. Similarly, Deason (1975) and Johnson (1981) concluded that grazing was not important to the phytoplankton populations in the Yaquina estuary, Oregon. Taguchi and Fukuchi (1975) reported that the loss of phytoplankton by grazing was exceedingly low in shallow Akkeshi Bay, Japan, and Bakker and dePauw (1975) indicated that zooplankton grazing was not a major factor in controlling algal crops in estuarine waters of the Netherlands.

On the other hand, transport of phytoplankton carbon through the Columbia River estuary was important. Import into region 8 was over twice the in situ daylight primary production, for example, and 3.5 times our best estimate of the 24-hr production. Export to the ocean was 36% greater than in situ daylight production and 56% greater than 24-hr production. The estuary thus acts mainly as a conduit for the transport of chlorophyllous particles to the sea and probably secondarily as a trap for conversion of viable phytoplankton cells to detrital carbon, which then either sinks to the estuary bottom or is itself transported to the ocean.

The fraction of viable cells converted directly to detrital carbon in the estuary was difficult to evaluate with the data in hand. The 36,654 (or 45,541) mt C yr^{-1} unaccounted balance could either be particulate or dissolved, or some combination. We have no concomitant measurements of dissolved organic carbon (DOC), but from Bristow et al. (1985) and unpublished data of our own we can compute a summer mean value (± 1 SD) of 1.67 ± 0.37 g DOC m^{-3} for the estuary, with no apparent changes at the freshwater–brackish water interface. From Dahm et al. (1981), the annual average DOC concentration at a station 128 km from the estuary mouth was approximately 2 g m^{-3}. The highest phytoplankton-derived organic carbon (PPOC)

concentration in summer was 0.68 g m^{-3}, and the summer average through the estuary was 0.44 g m^{-3}, which was in the same range as the standard deviation around the mean DOC concentration above. Thus, any possible conversion of PPOC to DOC cannot be resolved with the data in hand. However, we can calculate the import of total particulate organic carbon (TPOC) into region 8 and the subsequent transport into region 1 in a manner identical to that for phytoplankton carbon transport (we cannot calculate export to the ocean because we have no data on TPOC concentrations in the adjacent ocean). Recalculating TPOC transport from data in Lara-Lara (1982), using our regions and exchange rates, yielded a TPOC transport of 207,935 mt C yr^{-1} into region 8, and 200,615 mt C yr^{-1} into region 1. The near-equal values of transport into the two regions suggested little net loss of particulate carbon during estuarine transit; however, we know there was appreciable loss of PPOC, particularly at the freshwater–brackish water interface in summer (Table 5). PPOC is a part of TPOC. The lack of appreciable change in TPOC through the estuary, coupled with the documented changes in PPOC, suggested that PPOC was converted principally to detrital particulate organic carbon (DPOC) during the short transit time through the estuary. Thus, the unaccounted 36,654 (or 45,541) mt C yr^{-1} seemed to be mainly DPOC. If grazing loss was considered to be the maximum 5172 mt C yr^{-1}, rather than the median 1893 mt C yr^{-1}, the DPOC transport was still 33,375 (or 42,262) mt C yr^{-1} [only 9% (or 7%) less than DPOC transport with the median grazing loss considered].

We do not infer from the above calculations that freshly converted DPOC is all immediately swept toward the sea. Some likely sinks to the bottom for varying periods of time; however, some bottom DPOC of unknown age must be resuspended and transported to reasonably compensate the settled quantity over an annual cycle, because TPOC transport was generally invariate through the estuary. It must also be realized that all of the DPOC transiting the estuary or sinking to the bottom is not converted from PPOC, but some comes from runoff from land and from decomposition of marsh litter that makes its way into the main axis of the estuary. Detailed examination of the dynamics of DPOC must await further data, particularly from the tidal flats and marshes bordering the Columbia River estuary.

ACKNOWLEDGMENTS

Sandy Moore aided us immeasureably in all aspects of this work, and this aid is gratefully acknowledged.

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